

## CHEMICAL ORIENTATION OF BROWN BULLHEADS, *Ameiurus nebulosus*, UNDER DIFFERENT FLOW CONDITIONS

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**Abstract**—The spatiotemporal information in chemical signals provides critical information for organisms during chemical orientation. Information in chemical signals is influenced by the hydrodynamic conditions of the environment. Hydrodynamically distinct environments will contain different types of information, which will influence how organisms orient. This study was designed to examine how the orientation behavior of the brown bullhead (*Ameiurus nebulosus*) is influenced by flow regime. The experiment was conducted in a flume under two different flow conditions. Treatments consisted of control (no odor) and plain gelatin (odor). Percent success, swimming speed, turning angle, heading angle, heading angle upstream, and net-to-gross ratio were analyzed. Brown bullheads were 100% successful in finding the odor source under no flow and 57% successful in flow. Bullheads swam differently in the no-flow condition when compared to the flow condition. Since, these fish did not orient the same under different flow conditions, it appears that hydrodynamics plays a role in shaping their behavior.

**Key Words**—Chemical orientation, catfish, swimming behavior, hydrodynamics, chemical signal.

### INTRODUCTION

For many organisms, chemical signals are important sources of information that influence behaviors such as orienting toward food, attracting mates, avoiding predators, or determining social status (Lewis and Gower, 1980; Croll and Chase, 1980; Carr, 1988; Tierney and Atema, 1988; Breithaupt and Atema, 1993; Chivers and Smith, 1993; Sorensen and Scott, 1994; Hazlett, 1994; Chivers et al., 1996; Zippel et al., 1997; Bradbury and Vehrencamp, 1998). For instance, starfish are able to

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respond to a chemical stimulus and orient toward a food source in no-flow conditions (Moore and Lepper, 1997). Ovaries from female frillfin gobies develop a chemical that elicits courtship behavior in males, even in the absence of females (Tavolga, 1956). Western toad tadpoles (*Bufo boreas*) are able to recognize predator odors. They will display antipredator behavior when exposed to chemical cues from familiar predators, but will not display this behavior toward unfamiliar predators (Kiesecker et al., 1996). Yellow bullheads have been found to use chemical signals in recognizing individuals and associating odors with rank in hierarchies. Subordinate fish will avoid an area of an aquarium where water from the tank of a dominant fish has been introduced, even though the dominant fish is not present (Bardach and Todd, 1970).

One of the better-studied aspects of chemical signals is chemical orientation. Chemical orientation is defined as the directional movement of an organism toward an odor source (van der Steen and Maat, 1979). This orientation behavior is also observed in a variety of terrestrial organisms (Kennedy, 1986; Belanger and Arbas, 1998; Willis and Arbas, 1998; Takken et al., 1997). Aquatic organisms, in particular, have the ability to orient toward food, mates, home streams, parents, or offspring (Bardach et al., 1967; Tosi and Sola, 1993; Atema et al., 1980; Stabell, 1992; Weissburg and Zimmer-Faust, 1994). During orientation, fish exposed to chemical stimuli, such as food, display characteristic maneuvers that help them locate the odor source. Dogfish use a figure-eight pattern when searching for food (Parker, 1912), whereas sea robins use an s-shaped or zigzag search pattern when swimming up an odor gradient (Bardach and Case, 1965).

In order for chemical orientation to occur, an organism must be stimulated by a putative cue and must extract directional and distance information from it. Distance and direction information can be gained from a variety of cues, such as wind, flow direction, electroreception, and chemicals (Able, 1991). In the case of a chemical signal, there are two main characteristics that can provide information: quality and quantity of the signal. The quality is the type of chemical compounds that are stimulatory for that organism. It provides the organism with information on source type, i.e., food, predator, and reproductive condition (Sorensen et al., 1989; Schwenk, 1995; Carr et al., 1996; Rasmussen and Schulte, 1998; Swaisgood et al., 1999). For example, gravid garter snake females release non-volatile methyl ketones from cutaneous glands along the ground as they travel, providing information to males, which follow the females (Mason et al., 1989). Cichlids secrete proteinaceous mucus from their bodies, which maintains contact between the brood and parents, as well as provides food for the young (Barlow, 1974). Several common metabolites of low molecular weight have been found to be feeding stimulants (Carr, 1988). Other types of metabolites such as polyketides or alkaloids are feeding deterrents (Carr, 1988).

The quantity of chemical signals and their distribution in time and space can provide distance and direction information (Atema, 1988; Moore and Atema,

1991; Moore et al., 1994; Murlis, 1986, 1987; Murlis et al., 1992; Vickers, 2000; Zimmer-Faust et al., 1995). At macroscopic size scales, the spatial and temporal information in a chemical signal is structured primarily by fluid flow (Moore et al., 1994; Vickers, 2000). When an odor is released, the concentration fluctuates, creating a signal that is patchy in space and time. This patchiness consists of intermittent plumes in the water column with patches of high, low, or zero odor concentration. As the odor plume moves away from the source it spreads horizontally and vertically. (Murlis and Jones, 1981; Zimmer-Faust et al., 1995; Finelli et al., 1999; Moore et al., 2000). The degree of patchiness is influenced by the hydrodynamic conditions of the particular flow environment (Moore et al., 1994; Weissburg, 1997). Environments with different flow characteristics will consequently have different signal characteristics (Moore et al., 2000). In order to orient efficiently, animals need olfactory behaviors and physiological properties of sensory systems that can extract information from odor fluctuations (Moore et al., 1994; Atema, 1995).

Catfish provide an excellent opportunity to address questions concerning the influence of flow on orientation behavior. Ictalurid catfish are a model system for examining the role of chemical signals in orientation. Many of the species are nocturnal in habit and found in habitats of slow-moving or still waters with poor visibility, whereas others are found in turbulent flow conditions. For example, brown bullheads (*Ameiurus nebulosus*) are typically found in no-flow or low-flow conditions (backwater areas of rivers, ponds, and lakes). These fish are morphologically suited for environments dominated by chemical information (Bardach and Todd, 1970). Their bodies are covered with thousands of external taste buds, as well as dense concentrations on the barbels (Bardach and Todd, 1970; Atema, 1971). The physiological aspects of olfaction and gustation in channel catfish and bullheads have been extensively studied (Caprio and Raderman-Little, 1978; Caprio and Byrd Jr., 1984; Caprio et al., 1989; Miyamoto et al., 1990; Kang and Caprio, 1991; Restrepo et al., 1990; Kanwal and Finger, 1997). However, the behavioral aspects of orientation have not been thoroughly studied. The purpose of this study was to test the hypothesis that catfish, which are adapted to a particular hydrodynamic condition, orient more successfully to an odor source in their normal hydrodynamic environment than in one to which they are not adapted.

#### METHODS AND MATERIALS

*Animals.* Brown bullheads (*Ameiurus nebulosus*) were bought from Northeast Aquatics and placed in community tanks for observation over several months. This observation time allowed the fish to become accustomed to their new environment. The mean size for bullheads was  $21 \pm 0.72$  cm. Fish were kept on a reversed 12L : 12D schedule. Fish from the community tank were randomly caught and

isolated in 10-gal tanks ( $25 \times 31 \times 51$  cm) for at least two weeks before experimentation. Temperature ranged from 55 to 60°F in the winter and to 65°F in the summer. Both community and isolation tanks were routinely cleaned. Diet consisted of goldfish food (Wardley Pond Ten), fish (whitefish or pollack), and catfish food (Net Profit fish food). Fish were fed with the main light on either late morning or early afternoon. Past research has shown that brown bullheads have the ability to exhibit diurnal phasing, showing no or less-pronounced negative phototactic behavior (Eriksson 1978; Eriksson and van Veen, 1980). It has also been shown that, in nature, when there is a rise in water level, catfish will forage during the day (Pflieger, 1975). Valentinčič et al. (1994) reported that channel catfish fed uninhibitedly in a lighted room within a week of being moved to a test tank.

*Test Arena.* All orientation experiments were conducted in a plywood flow tank ( $244 \times 57.3 \times 62$  cm; Figure 1). The test section of the flume was 212 cm long. The start gate was placed at the downstream section of the tank. This holding area was  $26.5 \times 58$  cm. The odor source was placed at the upstream section of

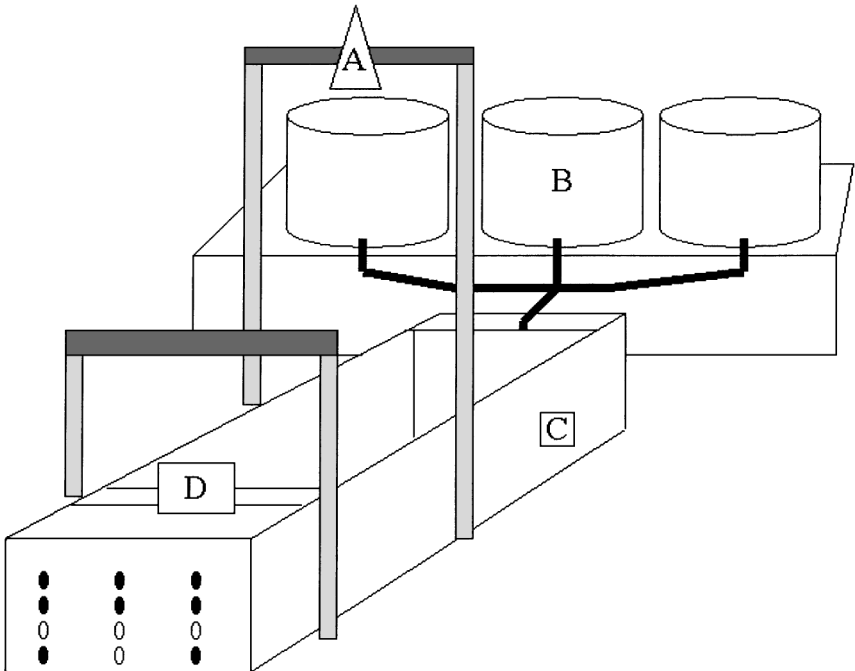


FIG. 1. Diagram of the experimental tank. The triangle with A shows camera location; B represents the head tanks. The flow tank is labeled C and the start gate is labeled D.

the tank, which was placed at least 15 cm away from the upstream collimator. The source was 29 cm from each side of the tank and 22 cm from the head collimator. The odor source was 197 cm away from start gate. This allowed test subjects to move beyond the odor source. Water was kept at a constant depth of 16 cm. Flow velocities were calculated by visually timing a neutrally buoyant object's movement over a given distance five times and taking the average time in seconds. Flow velocity during the flow trials was  $4.2 \pm 0.88$  cm/sec and  $0.0 \pm 0.0$  cm/sec during the no-flow trials. Flume water was stored in head tanks above the flow tank and was allowed to age for two days before use. Head tanks held a total of 115 gal for refilling the flow tank during no-flow trials and providing the water for the gravity feed in the flow trials. After each trial, the tank was drained completely and fresh and distilled water was used to rinse down the tank before the next trial.

*Odor Source.* Treatments consisted of a control (empty mesh bag), plain gelatin, or fish gelatin. Gelatin has been used as a source of food and a method of delivery for specific amino acid supplementation to test subjects (Keen, 1982; Sarwar and Ratnayake 2000; Buentello and Gatlin III, 2000). Preliminary data showed that plain gelatin produced a stronger response from the research subjects than fish gelatin. Those that did respond to the fish gelatin did not show any overall difference in swimming parameters, and so the data with the fish odor were dropped from further analysis. The odor sources were placed into a mesh bag, which was tied to the head collimator by a 16-cm piece of clear fish line. Weights (6 g) were used to hold down the bag. Four Knox gelatin packages were added to four cups of hot water and placed into a plastic container (30 × 16 cm). This was stirred together until everything was mixed. It was then placed into the refrigerator. Gel blocks (2.5 × 4 × 2 cm) were cut from the larger dish of prepared gelatin. The odor treatment was placed into the tank at least 30 sec before the start gate was opened.

*Dye Trials.* Dye trials were carried out for the no-flow treatment to quantify how fast the odor moved in the flume. 1- × 2-cm squares were measured, drawn, and numbered on the floor of the tank with a permanent marker. Grid sheets were used for visual marking of the odor trail during a 5-min trial. The dye gel block was made following the same recipe as the odor gel blocks (Moore and Lepper, 1997). The dye gelatin was cut into 1- × 2-cm squares instead of the size used for the experiment because the dye blocks kept breaking in half. Once placed into the flume, dye filaments would come off the gel block before timing and dissipate quickly, moving about the tank. Once the block was sitting on the bottom of the tank, timing started and the number of 1- × 2-cm squares covered in dye were marked out on the grid sheet until the 5-min experimental period was up. The number of squares was counted and the average dye movement in no flow was calculated to be  $0.056$  cm<sup>2</sup>/sec.

*Experimental Design.* Fish were starved for two days before they were used in a trial, and each was given a week between tests to avoid any learning biases. Separate groups were tested for flow ( $N = 7$ ) and no flow ( $N = 7$ ); however, a single fish was randomly tested under all odor conditions within a single flow condition.

Presentation of odor was randomized and each fish was given a week between trials. A randomly chosen fish was placed into the start gate section of tank and given 20 min to acclimate. After 20 min fish were resting on the bottom of tank in the start section. The start gate was slowly opened and left open so fish had the option to stay in this section. The acclimation time was chosen based on other fish research (Bardach et al., 1967; Ellingsen and Døving, 1986; Nevitt, 1991; Giaquinto and Volpato, 1997; Smith, 2000), which examined a variety of different acclimation times and fish behaviors. A camera (Quazar model VM-52 SVHSC CCD) was set 3 ft above the flow tank and connected to a Hi-Fi Stereo Hi 8 recorder (NTSC EV-C100). Recording was carried out under red lights. The no-flow trials were taped for 20 min, and the flow trials were taped for 4.5 min or until the catfish first hit the odor source. Behavioral trials were conducted until an animal successfully located the odor source. A trial was defined successful when the test subject touched the odor source with its mouth.

*Data Analysis.* The Peak Motus Motion Analysis System was used to digitize orientation paths under both flow conditions. A fish's position was digitized every second. Animals took an average of 30 sec in no flow and 32 sec in flow to locate the odor source. Therefore, control groups were digitized for 30 sec for the no flow and 32 sec for the flow. The coordinate ( $x, y$ ) data were then put into an in-house standard orientation template to calculate speed, turning angle, heading angle, heading angle upstream, and net-to-gross ratio (Moore et al., 1991) (Figure 2). When calculating the angles, the right and left angles were not differentiated; hence all angles fall between 0 and 180°. This type of analysis allows us to perform statistical analysis with standard linear statistics (e.g., MANOVAs). Circular statistics are slightly more conservative than MANOVAs. Performing an analysis using linear statistics allows us to analyze the fine details of fish movement patterns. The consequences for a linear analysis is that it is possible for a zig-zag pattern typically found in moths to have a mean heading angle of 60°. For statistical analysis, a single mean for each parameter was calculated from the total orientation path. The total path means were subsequently used for all statistical analysis as the data points that were put into the two-way MANOVA. A two-way MANOVA was used to analyze speed, speed towards source, turning angle, heading angle, heading angle upstream, and net-to-gross ratio for bullheads. All significant  $P$  values were set at 0.05. A Fisher's exact test was used to analyze percent success.

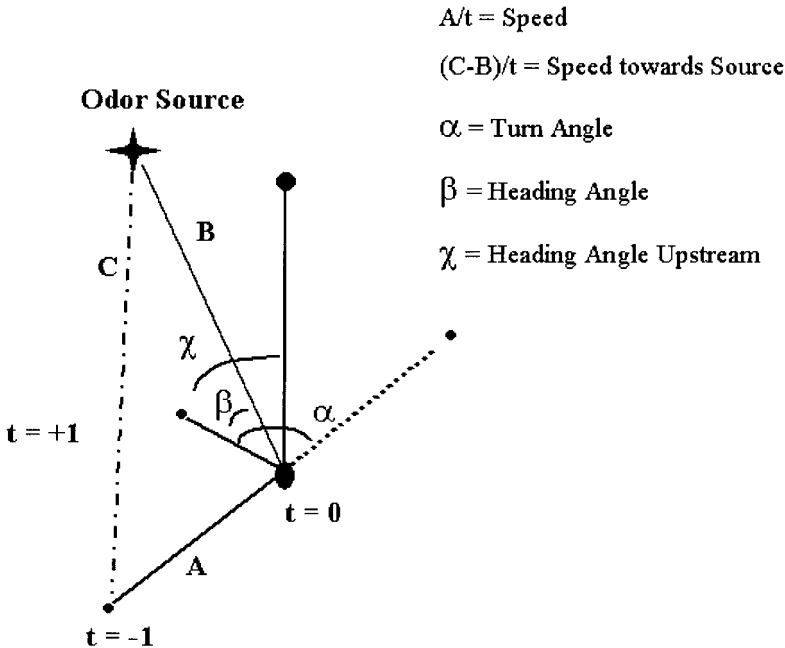


FIG. 2. Diagram shows three successive positions ( $t = -1, 0,$  and  $+1$ :●) on a hypothetical orientation path used to define behavioral parameters. The dashed line represents the catfish's projected path (if it continued in a straight line), from which a turn angle value ( $\alpha$ ) at point  $t = 0$  is calculated. The solid line (B) represents the straight line to the odor source (four point star) from which heading angle relative to the odor source ( $\beta$ ) is calculated. The unlabeled line represents the path that is straight upstream, from which the heading angle relative to upstream ( $\chi$ ) is calculated. Swimming speed (A) is the distance moved from time point  $t = -1$  to  $t = 0$ . The difference between distance to the odor source at time  $t = -1$  (dash-dot line, C) and distance to the odor source at time  $t = 0$  (solid line, B) is the swimming speed toward the source.

RESULTS

*Success at Finding Odor Source.* Brown bullheads were successful in locating the odor source under both flow and no flow conditions. Seven of seven brown bullheads (100%) found the odor source under no flow. Four of seven bullheads (57%) were successful in finding the odor source under flow. The Fisher exact test showed no significant difference between the two odor treatments (Fisher exact, one-tailed;  $P > 0.09$ ).

*Qualitative Description of Orientation Behavior.* In no flow, catfish swam in a more linear fashion when odor was present. In general, fish made fewer turns

while swimming toward the odor source. Fish were seen mouthing the mesh bag once they found the odor source. During the control trials, fish swam around the tank and did not investigate the mesh bag. They could be seen swimming along the edges more than individuals in the odor trials. The catfish pathway was more circuitous under flow for both treatments. An example of swimming paths for each treatment is illustrated in Figure 3.

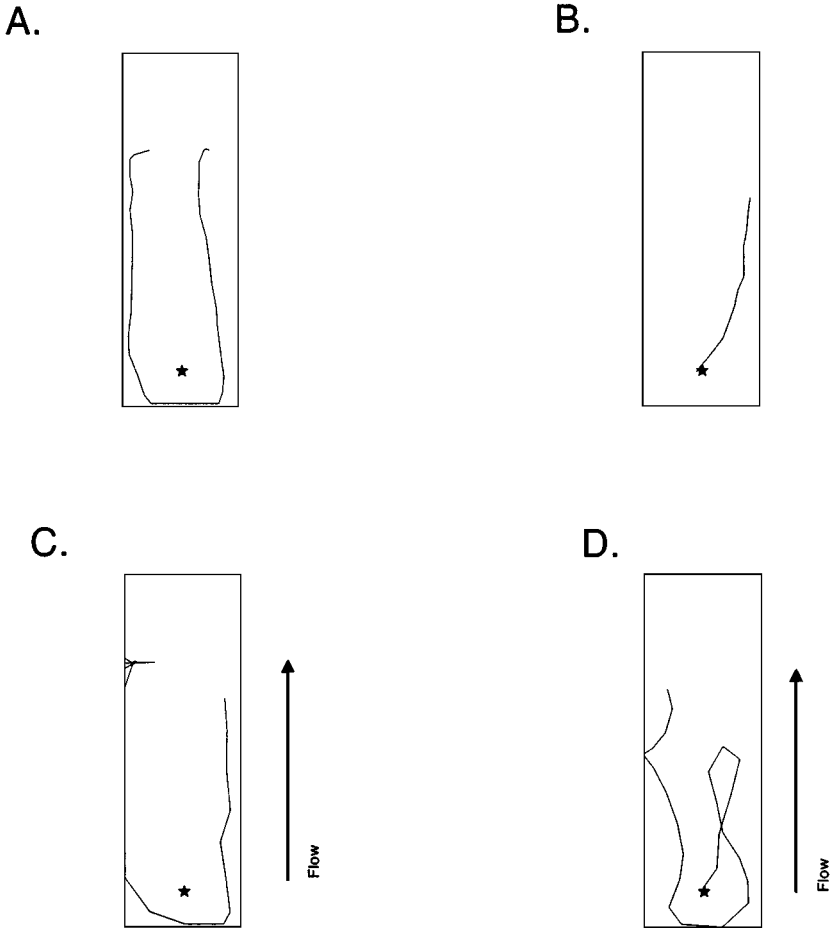


FIG. 3. (A) A representation of the path made by a bullhead under no flow and no odor source. (B) A typical path made by bullheads with an odor source in no flow. (C) A representation of the path made by a bullhead under flow without an odor source. (D) A typical path made by bullheads with an odor source under flow. The star represents the odor source (or contact), and the arrows illustrate the direction of the flow.

*General Effect.* Brown bullheads oriented differently when an odor was present (MANOVA, Rao's  $R = 7.04$ ,  $P < 0.01$ ). They also oriented differently under flow and no flow (MANOVA, Rao's  $R = 5.59$ ,  $P < 0.02$ ). This effect was seen in the net-to-gross ratio, swimming speed, heading angle upstream, heading angle toward source, and turning angle toward source. The post-hoc analysis provided a more detailed view of this behavior.

*Effect of Flow and Odor on Swimming Speed.* Brown bullheads swam significantly faster under flow ( $6 \pm 2$  sec) conditions than during no flow ( $14 \pm 2$  sec) in the control trials (Figure 4; Newman-Keuls post-hoc,  $P < 0.02$ ). In addition, brown bullheads also swam faster when stimulated with an odor source in flow ( $13 \pm 1$  sec) than no flow ( $19 \pm 1$  sec) (Newman-Keuls post-hoc,  $P < 0.005$ ).

*Orientation Paths.* Brown bullheads swam a straighter path when an odor was present (indicated by a higher net-to-gross ratio) in the no flow conditions ( $0.85 \pm 0.1$ ) (Figure 4; Newman-Keuls post-hoc,  $P < 0.001$ ) as compared to the flow condition ( $0.19 \pm 0.04$ ). Brown bullheads swam more randomly in no flow ( $0.22 \pm 0.09$ ) and flow ( $0.10 \pm 0.01$ ) controls (blanks) (indicated by the lower net-to-gross ratio) (Newman-Keuls post-hoc,  $P > 0.05$ ). Turning angle toward source was lower for brown bullheads during odor trials in no flow ( $16 \pm 3^\circ$ ) condition than flow ( $35 \pm 2^\circ$ ) (Figure 5; Newman-Keuls post-hoc,  $P < 0.002$ ). However, there was no difference in turning angle for the control trials in no flow ( $24 \pm 8^\circ$ ) or flow ( $38 \pm 7^\circ$ ) (Newman-Keuls post-hoc,  $P > 0.05$ ). The heading angle relative to an odor source measures the accuracy of an organism's movement toward an odor source. Brown bullheads had a lower heading angle while orienting in no flow ( $23 \pm 9^\circ$ ) than flow ( $68 \pm 4^\circ$ ) condition (Figure 5, Newman-Keuls post-hoc,  $P < 0.001$ ). The control group in no flow ( $55 \pm 15^\circ$ ) did not differ from the control group in flow ( $76 \pm 4^\circ$ ) for heading angle toward source (Newman-Keuls post-hoc,  $P > 0.05$ ). Brown bullheads had a lower heading angle upstream when orienting to an odor source in no flow ( $23 \pm 10^\circ$ ) condition (Figure 5, Newman-Keuls post-hoc,  $P < 0.02$ ) as compared to flow ( $61 \pm 10^\circ$ ). There was no difference in heading angle upstream between the control group in no flow ( $57 \pm 16^\circ$ ) and flow ( $75 \pm 5^\circ$ ) (Newman-Keuls post-hoc,  $P > 0.05$ ).

## DISCUSSION

The results of this experiment indicated two important conclusions for catfish orientation. First, it confirmed our expectations that brown bullheads would orient more successfully under no-flow conditions compared to flow conditions. Although not significantly different, brown bullheads appeared to have a higher success rate in finding the odor source under no flow (100%) than flow (57%). These trends are in the direction of our hypothesis, but the conservative nature of the Fisher exact test does not show significant differences between these two

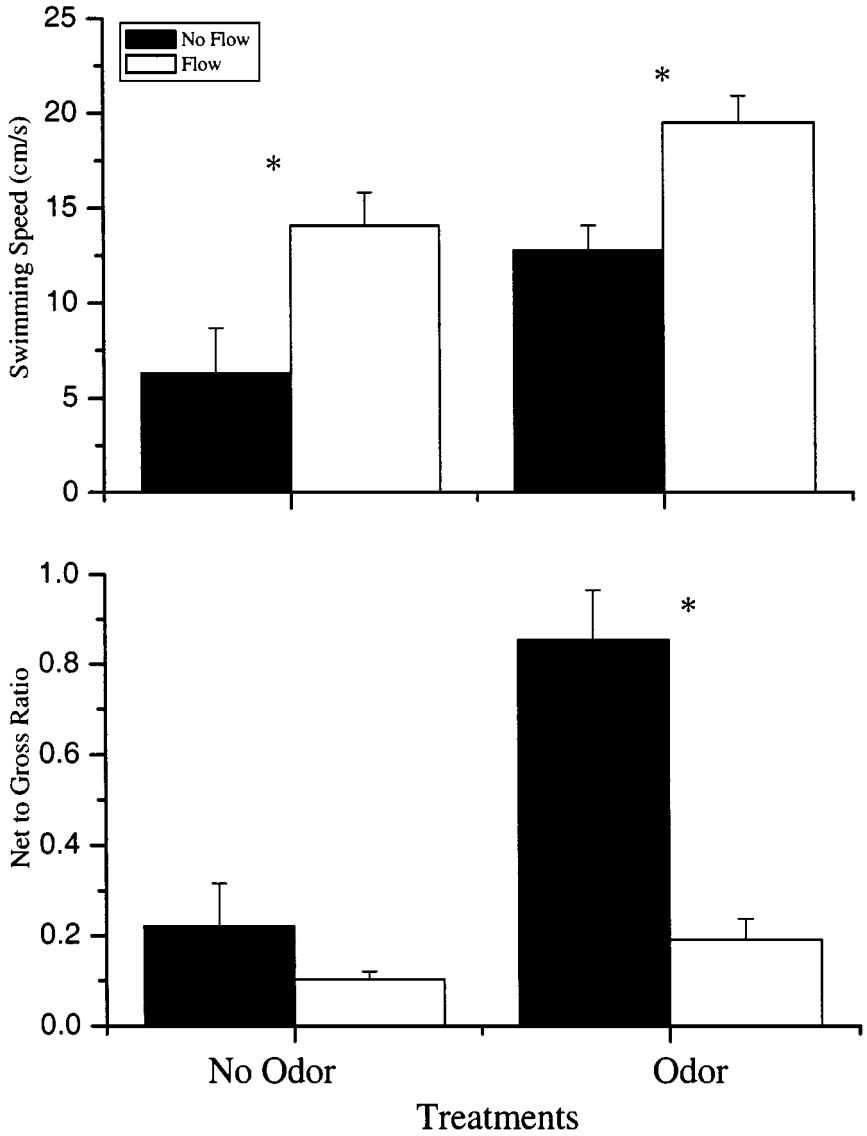


FIG. 4. The upper graph illustrates the swimming speed of bullheads in no-flow (black) and flow (white) conditions. The bottom graph is the net-to-gross ratio of bullheads in no flow (black) and flow (white). An asterisk indicates a significant difference using MANOVA followed by post-hoc test.  $N = 7$  for each flow treatment.

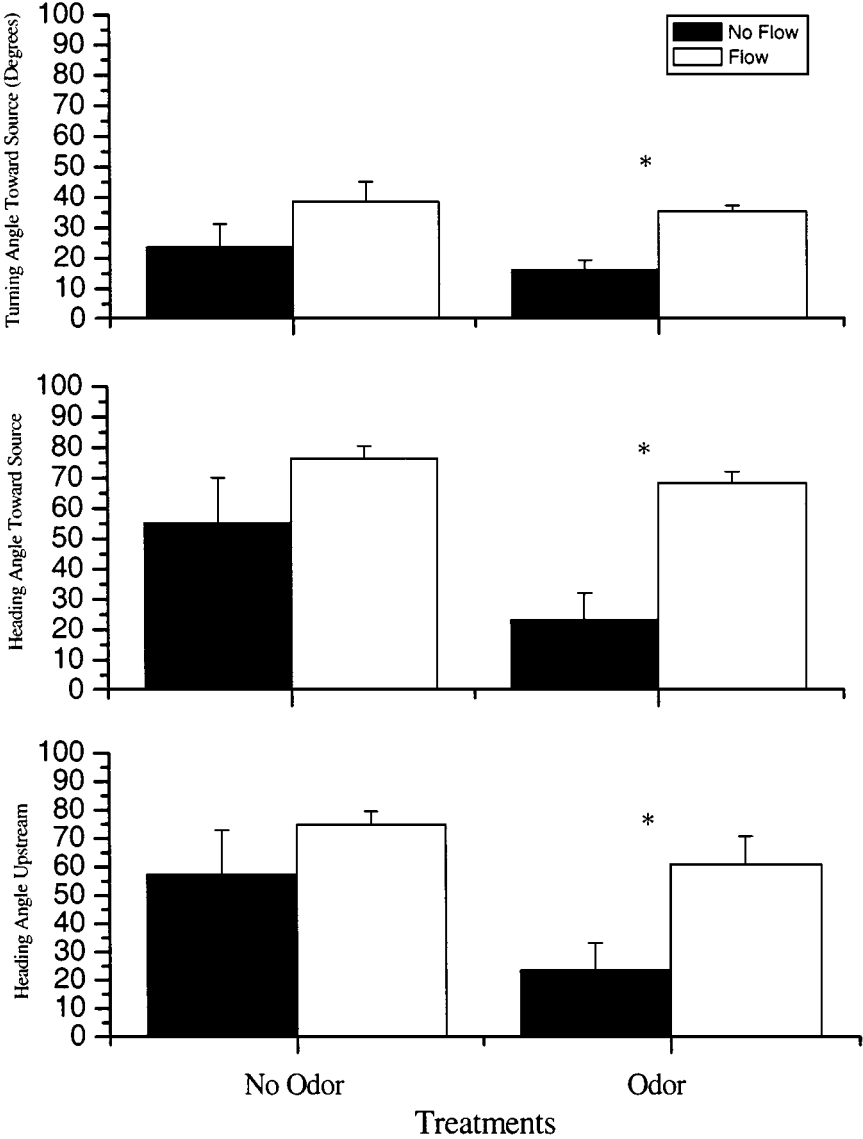


FIG. 5. The upper graph illustrates the turning angle of bullheads in no-flow (black) and flow (white) conditions. The middle graph is the heading angle toward the source of bullheads in no flow (black) and flow (white). The bottom graph shows the heading angle relative to upstream of bullheads in no-flow (black) and flow (white) conditions. The asterisk indicates a significant difference using a MANOVA followed by a post-hoc test.  $N = 7$  for each flow treatment.

treatments. We expect either a less conservative test (chi squared) or a larger number of replicates would show significance. Second, it showed that bullhead orientation was influenced by changes in the flow conditions. A statistical interaction was found between the flow/no-flow treatment and the odor treatment with regard to swimming speed. During odor stimulation, bullheads swam faster in the flow condition when compared to the no-flow condition. Since both flow and odor modulated the bullhead's orientation response, this statistical effect suggests that bullheads may use some type of an odor mediated rheotactic response.

The orientation paths exhibited by bullheads during chemical stimulation were different for the flow and no-flow conditions. Bullheads had more linear orientation paths under no-flow conditions than in flow conditions. Post-hoc analysis showed that bullheads did not swim differently in no-flow or flow in the absence of odor. Other spatial aspects of orientation, such as turning angle, heading angle, and heading angle upstream were smaller under no flow when compared to flow conditions. This indicates that bullheads made smaller course corrections when orienting to the odor source under no flow than under the flow condition. Larger angles in the control trials indicate greater course correction, therefore illustrating a less directed swimming. There was no difference between flows in any of these parameters when odor was absent from the trials. Overall, the orientation angles and the net-to-gross ratio indicated that bullheads swam directly to the odor source under no flow. These results suggest that bullheads may be performing a gradient type of search in no-flow conditions, which supports past research on catfish (Bardach et al., 1967). The no-odor results also indicate that the shape of the tank did not influence the swimming behavior of the fish. If the tank were to constrain orientation behavior, we would expect that both no-odor controls would show similar spatial effects.

In the odor/flow treatment, catfish could be gathering information by the distribution of the odor patches and possibly some information on flow direction. Bullheads have been found to be sensitive to odor concentration differences (Johnsen and Teeter, 1980) and have also been found to orient successfully under no-flow to a liquid odor source (Bardach et al., 1967). The odor source used in this study diffused slowly based on dye trials, but patches of odor source came off while placing the source in the tank. These patches could have diffused out in the water column, setting up patches of odor for the bullheads to encounter as they come out of the start gate. Gelatin has several amino acids (Bohidar, 1997; Lüpke and Brückner, 1998) [such as arginine and alanine (Caprio et al., 1993; Ivanova and Caprio 1993; Valentinčič and Caprio, 1994)] that have been found to be stimulatory to catfish.

In flow conditions, turbulence directly impacts odor distribution and indirectly influences an animal to modify its locomotor behavior during orientation (Weissburg and Zimmer-Faust, 1993). Eddies that are formed by turbulence interact

with the odor plume, influencing the spatial and temporal fluctuations of the odor concentration (Moore and Atema, 1991). In addition to flow speed, substrate can also influence the hydrodynamics of a habitat. In a study detailing the influence of habitat on chemical signal structure, Moore et al. (2000) found that chemical signals have different spatial and temporal information on different substrates such as sand, cobbles, or gravel. Presumably, the level of turbulence in a system directly impacts the frequency of odor pulses that are measured in an odor plume (Moore et al., 2000). The modifications in locomotor behavior seen in the brown bullheads between the flow, and no-flow, could be due to either differences in the odor plumes or the flow affecting their swimming ability. Still, the results seem to indicate that the swimming behavior pattern seen is related to the distribution of the odor and not the flow regime. There were no significant differences between the controls in any of the orientation parameters, except speed.

An important hypothesis that has been put forth and is being supported by several studies states that organisms should have sensory systems and behaviors that are adapted to the specific sensory conditions of their environment (Wehner, 1987; Atema, 1988; Moore et al., 1991; Endler, 1995; Huber et al., 1997; Weissburg, 1997; Endler and Basolo, 1998; Kotrschal et al., 1998; Schneider et al., 1998; Land et al., 1999; Persons et al., 1999; Poling and Fuiman, 1999; Schneider and Moore, 2000). From this hypothesis we could predict that organisms should perform behavioral tasks more efficiently or more successfully when presented with conditions that are similar to their natural habitats. If we alter environmental conditions that structure sensory information, we would expect to find either changes in behavior or decreased success in performing a specific behavioral task. We found both of these results with brown bullheads.

This phenomenon has also been found with regard to orientation behavior in other species. For example, blue crabs (*Callinectes sapidus*) traveled upstream and at higher speeds toward a food source (clams) in smooth-turbulent flows (Weissburg and Zimmer-Faust, 1994). These behaviors changed when turbulence shifted from smooth to rough. In this case, crabs were slower and made more frequent stops. It was also found that rheotactic and chemical information are necessary for crab orientation (Weissburg and Zimmer-Faust, 1994). Crayfish (*Orconectes rusticus*) are able to use information from the temporal and spatial distribution of chemicals to make directional decisions. Differences were found in how fast they located a food source, time spent moving, and how fast they moved on different substrates. These differences in orientation behavior were based on the hydrodynamics associated with chemical signal structure (Moore and Grills, 1999). In moths, pheromone pulse frequency determines flight form of males in two phylogenetically distant moths, a noctuid (*Heliothis virescens*) and a pyralid (*Cadra cautella*) (Vickers and Baker, 1994; Mafra-Neto and Cardé, 1994, 1998). These moths fly faster and straighter to sources of high-pulse frequencies and slower and more zigzag to sources of low-pulse frequencies. Finally, tsetse flies (*Glossina pallidipes*) show a

stepwise orientation approach, which allows them to assess wind direction between flight bursts (Bursell, 1984).

In summary, this study demonstrates that bullheads can orient successfully to an odor source and are successful under flow conditions that are similar to their natural environment. It also suggests that bullheads may be generalists in their orientation behavior. Since the spatial pattern of orientation was different in the two flow conditions tested, they may be able to switch search strategies depending on the flow condition and signal structure. This suggests that the hydrodynamic environment may be an important factor in the shaping of an organism's chemosensory behavior. However, further studies need to be done to distinguish if bullheads are really using different search strategies under different flow conditions. More studies are also required in order to understand how bullheads are finding the odor source under no flow.

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